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始巨鳄类(兽孔目,下孔亚纲)在中国的首次发现

——甘肃玉门晚二叠世脊椎动物群系列报道之四[1)]

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摘要 记述了始巨鳄亚目的一个新属新种祁连双列齿兽(*Biseridens qilianicus*)。标本产自甘肃玉门大山口上二叠统的西大沟组。*Biseridens* 以中等大小的头骨,短的眶前区,粗大的顶骨结节和大的顶孔,形态独特的颊齿和双排齿列,有别于体型硕大,肉食习性的 *Eotitanosuchus*。动物群的分析表明,大山口低等四足类动物群与俄罗斯上二叠统卡赞阶 II 带的脊椎动物组合有较为密切的关系。

关键词 甘肃玉门, 晚二叠世, 始巨鳄亚目 双列齿兽科

中图法分类号 Q915.864

始巨鳄(eotitanosuchids)是一类具大而重头骨的原始兽孔类。按照 Sigogneau-Russell (1989)在古四足类手册 17 分册的划分,始巨鳄兽类作为一个单独的亚目(Eotitanosuchia)只包括一科两属两种,它们是始巨鳄科(Eotitanosuchidae),奥尔森始巨鳄(*Eotitanosuchus olsoni* Chudinov, 1960)和佩剑伊万特龙(*Ivantosaurus ensifer* Chudinov, 1983)。化石都采自俄罗斯上二叠统卡赞阶的 Esheevo。本文依据一不完整的头骨和下颌所记述的祁连双列齿兽(*Biseridens qilianicus* gen. et sp. nov.),可代表一单独的新科归入始巨鳄亚目。这是此类动物在中国,也是在俄罗斯之外的首次发现,这一发现丰富了大山口动物群的组成。此前这一动物群仅有大鼻龙型类的 *Belebey vegrandis*(李锦玲等,1995),恐头兽类的玉门中华猎兽(*Sinophoneous yumenensis*)(程政武等,1996)和利齿狭头兽(*Stenocybus acidentatus*)(程政武等,1997)被报道。这一发现更进一步证明了大山口动物群与俄罗斯 II 带脊椎动物之间的联系,同时为探讨早期兽孔类的系统发育提供了素材。

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始巨鳄亚目　Eotitanosuchia Boonstra，1963

双列齿兽科　Biseridensidae Fam. nov.

特征　见科型属 *Biseridens* 的特征。

双列齿兽　*Biseridens* Gen. nov.

词源　*Biseri-*拉丁形容词“二列的”，*dens* 拉丁词“齿”。

特征　原始的食植物或杂食性的兽孔类。头骨中等大小；眶前部短而狭；眶间部下凹，沿中线具额骨中嵴；眶间部宽度小于间颞部宽度；颞孔大于眼孔，椭圆形的顶孔极大，位于粗大的顶骨结节之上；眶后骨下突未伸达颧弓，眶后骨后部在颞孔内形成的凹，为下颌收肌的接触处；间顶骨高而窄，后耳骨与方骨相接；腭骨和翼骨具簇状的小齿，翼骨横缘无齿；下颌关节位于头骨的最后端，低于下颌齿列；颊齿形态特殊，后部颊齿呈双列，下颌齿式：I3C1PC15。

祁连双列齿兽 *Biseridens qilianicus* gen. et sp. nov.

(图版 I，II；图 1，2)

词源　*qilian* 化石产地祁连山的名称。

正模　一头骨后部和左下颌支后部(地科院地质所 V 362)。

副模　带有完整齿列的一对下颌支前部(古脊椎动物与古人类研究所 V 12009)。

产地及层位　甘肃玉门大山口，上二叠统西大沟组。

特征　同属的特征。

标本保存情况：头骨严重破损。吻端和右侧部断失，腭面未保存，但头骨顶面后部，左侧面后部和枕面基本完好。与头骨咬合在一起的左下颌支后部的腹缘破损。由于正模的左下颌支保存了包括齿列后部在内的齿骨以后的部分，而副模的左右齿列又保存完整，排除了它们属于同一个体的可能。副模的牙齿大小和齿骨宽度与正模的相应部位相当一致，推测副模与正模代表着相同大小的两个个体。将副模齿列后端与正模左下颌齿列后端重合组成一基本完整的下颌，其形态结构看上去无不妥之处(图 1B)。这样完整下颌的(可能)长度为 16 厘米。再以下颌的前端为准复原吻端的形态，得出完整头骨的(可能)长度 18 厘米。

标本记述　顶面(图 1A)：头骨埋藏时显然遭受侧向挤压，左颧弓向内压入，接近头骨中线，从顶面无法观察到。但侧向挤压对头骨顶面的影响不大，它基本保持左右对称。头骨保存部分的顶面形态为一近似的梯形，最大宽度位于头骨最后端的鳞骨部——这也是整个头骨的最大宽度。与始巨鳄类相似，它的间颞部宽度大于眶间宽度。眶间部明显下凹。顶孔大，椭圆形，位于粗大高耸的顶骨结节之上。头骨后缘呈一前凸的弧形，最后端亦在鳞骨部，它比头顶后缘的中点及枕髁要大大靠后。

左鼻骨仅保存了一长 3 厘米宽 1 厘米的后部，它的后端在眼孔前缘一线呈尖突状插入额骨。骨片表面具细小弯曲、浅沟状的雕饰。左前额骨基本完整，它外侧的泪骨受挤压移至它的下方，前额骨顶面外低内高，与鼻骨、前额骨相接的骨缝张开，使前额骨成为一块突

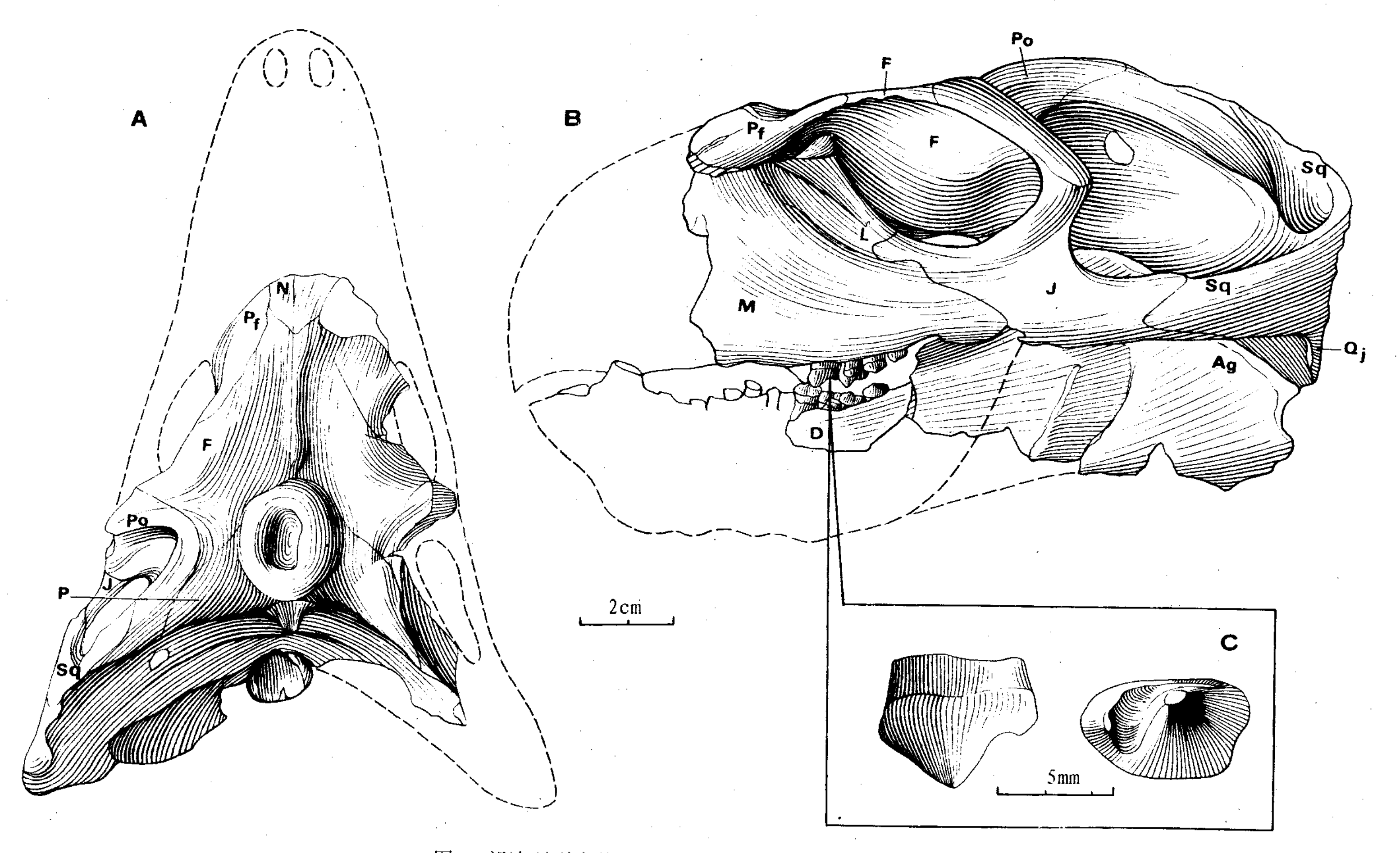


图1 祁连双列齿兽(新属新种)正模(IGCAGS V 362)

A. 头骨顶视；B. 头骨及下颌左侧视；C. 上颌颊齿外侧和嚼面视(简字说明见图2)

Fig.1 *Biseridens qilianicus* (gen. et sp. nov.) holotype (IGCAGS V 362)

A. Skull in dorsal view;. B. skull and lower jaw in lateral view; C. cheek tooth in lateral and occlusal view (abbreviation see Fig.2)

出于眼眶前上角的骨片。左右两侧都无法查明额骨与后额骨的骨缝（这点与始巨鳄类也十分相似），推测额骨宽大，它在眼眶上缘占据了相当的位置。眼眶边缘稍高，眶间部明显下凹。左右额骨缝合处形成一清晰但低矮的中嵴，该嵴将眶间部的凹陷分为左右两部分，但它并未伸达顶骨结节的前缘。虽然额骨后缘的骨缝不清，嵴的后端很可能标示着额骨的终结处。从顶面看眶后骨分隔了眼孔和颞孔。它的下突中止于眼孔后缘的中部，未伸达颧弓。眶后骨后突向后外侧延伸，中止在枕髁一线。顶视可见眶后骨在颞孔的前上角形成一明显的凹面，作为下颌收肌的起点。顶骨相对较宽，它的顶面形成一粗大高耸的椭圆形结节（长 2.5 厘米，宽 2.0 厘米，前高 1.3 厘米，后高 0.5 厘米），围绕着大的椭圆形顶孔。顶骨两侧稍向后外侧延伸。

侧面（图 1B）：头骨虽受侧向挤压，左眶前部略向内扭曲，眶后弓中部折曲，鳞骨稍向后移，但对侧面总体形态影响不大。颞孔大于眼孔。与原始兽孔类双节鳄（biarmosuchians）较小的颞孔比较，它是通过垂直方向的加长和前内侧角的向前扩展而得以加大的，这点与恐头类（dinocephalian）非常相似。如果前述正模与副模迭加复原的头骨形态无大问题，那这一动物具有较短的眶前部，长约 8 厘米，占头骨全长的 44%。

前颌骨和隔颌骨未保存，上颌骨和鼻骨的前半部断失，吻端的特征和外鼻孔的形态无从推测。保存的上颌骨后部呈三角形，与前额骨相接处似乎处于上颌骨的最高点，它的后缘自此点向后下方延伸，直至眼孔的下方。上颌骨的腹缘显示轻微的波曲。在前端破断处，可见一齿根深植于齿孔中，断面椭圆形，长径（前—后向）0.90 厘米，短径（唇—舌向）0.35 厘米。从其大小、所处的位置及延伸方向推测，这是上颌犬齿齿根的残留。紧随其后保存了一十分细小牙齿的齿根，断面近于圆形，它的长、短径分别为 0.25 厘米和 0.20 厘米。第 2 犬齿后齿未保存，一形态不规则的齿孔标示着它的位置。该孔的前、后分别有 0.50 厘米和 0.70 厘米的齿隙（diastema）。

在上颌骨腹缘最后一个向下突出的波峰处保留了 6 个基本完好的、形态特异的牙齿。它们呈双列分布，内侧的 3 个牙齿大于外侧的，且它们的排列比外侧的 3 个牙齿靠前。由于大小不一致（每列的牙齿自前向后都是中等—大—小），内外侧的牙齿并不一一对应。内侧 3 齿与外侧前 2 齿排列紧密，只有外侧最后一齿与它们间有小的齿隙（0.20 厘米）。此齿偏离齿列，稍向内侧移动。这些牙齿的断面呈长轴平行于齿列方向的椭圆形。齿冠低矮粗壮，靠近基部稍有收缩，齿冠高度小于前后径长度。自齿冠高度的中央，它的前外侧部分伸出一弯曲向内的齿尖，齿尖的唇侧凸度大于舌侧凸度。在齿冠高度的中央一齿平面围绕在齿尖的内侧和后方（图 1C）。这几个牙齿的形态明显地有别于肉食性兽孔类的单尖、侧扁、且向后弯曲的牙齿，也不同于食植性兽孔类带有舌侧齿踵（heel）结构的牙齿，但它与后者多少有些可比之处。很可能这些牙齿中部的齿平面即为齿踵发展的早期阶段。正模虽未保存前颌骨齿，前两个犬齿后齿的齿冠断失，但从大的犬齿及后部颊齿的复杂形态完全可以推知它具异齿型的齿列。

左侧泪骨稍有错位，它占据了眼眶前缘相当大的一段距离。与大部分早期兽孔类一样泪骨较短，由于上颌骨的背突与前额骨的相接将泪骨与外鼻孔远远地隔开。颧骨较为粗壮，它的三分支明显。前支位于眼眶下缘；上支构成眶后弓的下部，其顶端以一斜面插入到眶后骨的后内侧；后支近于水平地向后延伸，在颞孔的下缘与鳞骨下支的前端相接。

此接触点之后，颧骨在鳞骨的下内方继续后延了相当一段距离。鳞骨主体向后外方扩展，它在颞孔内眶后骨后支的后续部分形成一明显的嵴，嵴的上方为沿颞孔上缘延伸的一带状斜面。鳞骨的颧骨支与颧骨组成颞孔的下缘，它与上颌骨的腹缘几乎处在同一水平面内，这与异齿兽类(anomodontid)向后上方扬起的颧弓有很大差别。左方颧骨保存，但骨缝不甚清晰，它在鳞骨的后外角向下延至下颌关节。下颌关节并未前移，处于头骨的最后端，同时低于上颌齿列。

枕面(图 2A)：为一向前弯曲的凹面，上部较下部略向前倾，宽度大于高度。枕面各骨片间的缝合线都不很明晰，但从骨片的结构、表面纹理延伸的方向，尚可作出合理的推断。间顶骨为一直立的、形态不规则的骨片，高大于宽，其高度超过枕面高度的二分之一。具一中央纵嵴，嵴的上、下端较宽，中部较窄。向下它终止于间顶骨和上枕骨的骨缝，并未延伸进上枕骨。上枕骨宽而低，它从上部包围着枕骨大孔，由于右侧骨片的错动，枕孔的形态不甚分明，从左侧上枕骨下缘推断，它应是一不高但较为宽阔的拱形大孔。枕髁突出，呈圆三角形，三分明显，由左右外枕骨和下部的基枕骨组成。棒骨在枕面占据了相当大的面积，形态不规则。由后耳骨组成的副枕骨突粗壮，它的外端与方骨相接。方骨的形态不清，在此很难详细记述。头骨顶面的顶骨、眶后骨，侧面的鳞骨、方颧骨互相连接，宽窄不同地出露在枕面的边缘。

腹面：破损严重，无法识出其全貌。几块单独保存的骨片可反映其局部的构造。在枕髁之下保存了错位的右方骨关节部和与之相接的镫骨。镫骨较为粗壮，两端扩展，中间收缩。左上颌骨内侧保存了一小块腭骨，上面着生着 9 个大小不等但相当粗壮的腭骨齿，它们排列不整齐，呈簇状。该骨的内侧还有一薄的扇形骨片，代表着腭骨的前部。非常凑巧的是右侧同样保存了一小段上颌骨及与之相连的腭骨(图 2C)。在长仅 2 厘米的右上颌骨上，有 4 个上颌骨齿，齿尖不甚完整，但形态与左上颌骨后部颊齿一致，且排成内外两列。腭骨断块上亦有 10 个粗大的腭骨齿，内侧还有 5 个细小的腭骨齿。腭骨沿中线形成一窄沟。头骨腹面另一不完整的小骨块，在向上拱起的表面上有一簇小牙齿，推测它是右翼骨的一部分。后部可见弯曲的不具齿的翼骨横缘(图 2B)。

表1 (Table 1) 单位：厘米(cm)

头骨保存长度 length of incomplete skull	14.0
眶间部宽度 width of interorbital region	3.8
间颞部宽度 width of intertemporal region	4.8
眼孔(长×宽) size of orbit (length×height)	4.5×3.0
颞孔(长×宽) size of temporal fenestra (length×height)	5.0×5.0
下颌保存长度 length of incomplete lower jaw	10.5
下颌缝合部高度 height of symphysis region of lower jaw	3.5
下颌齿列长 length of lower dentation	7.5

下颌(图 2D、E)：由副模所代表的下颌前部保存完整。侧视齿骨前部低后部升高。下颌前缘自上向后下方倾斜。齿骨上缘呈波状弯曲，在犬齿之前向前下方倾斜，齿骨表面不

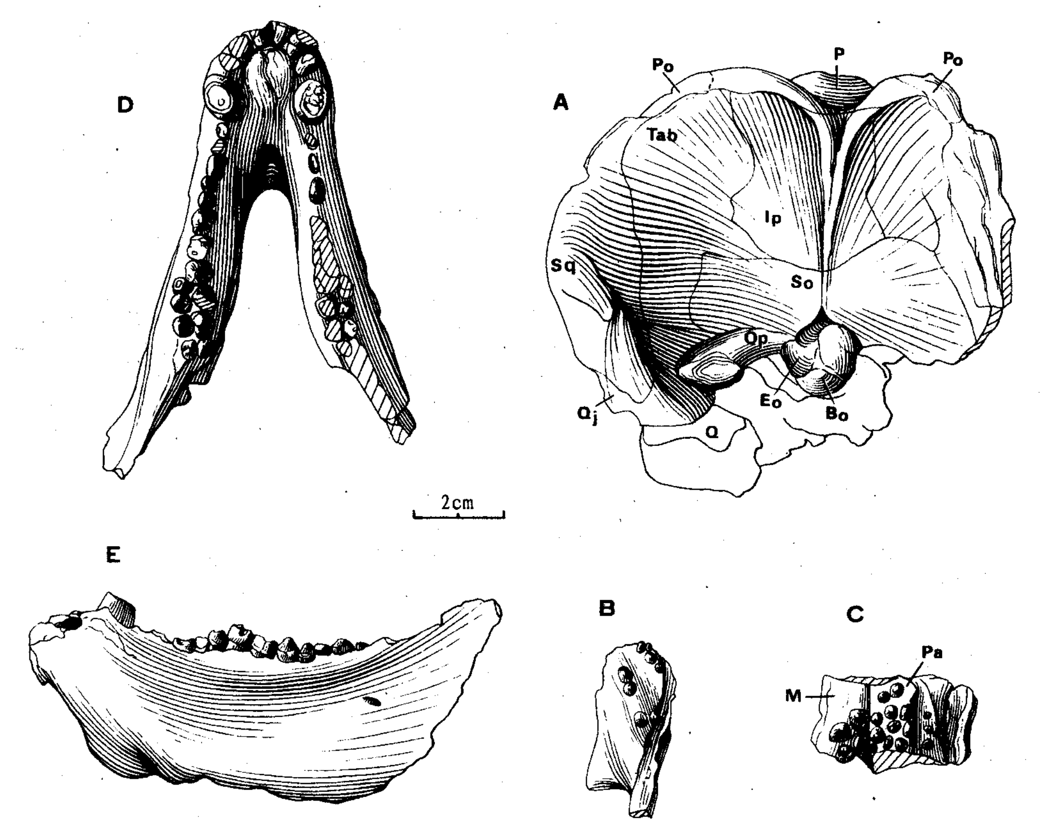


图 2 祁连双列齿兽(新属 新种) A.B.C. 正模(IGCAGS V 362)，A. 头骨枕面；B. 不完整的右翼骨；C. 部分右上颌骨和腭骨；D.E. 副模(IVPP V 12009)，D. 下颌背视；E. 下颌侧视

Fig.2 *Biseridens qilianicus* (gen. et sp. nov.) A.B.C. holotype (IGCAGS V 362), A. skull in occipital view; B. incomplete right pterygoid; C. incomplete right maxilla and palatine; D.E. paratype (IVPP V 12009), D. lower jaw in dorsal view; E. lower jaw in lateral view

Abbreviation: Ag. 隅骨 angular; Bo. 基枕骨 basioccipital; D. 齿骨 dentary; Eo. 外枕骨 exoccipital; F. 额骨 frontal; Ip. 间顶骨 interparietal; J. 颧骨 jugal; L. 泪骨 lacrimal; M. 上颌骨 maxilla; N. 鼻骨 nasal; Op. 后耳骨 opisthotic; P. 顶骨 parietal; Pa. 腭骨 palatine; Pf. 前额骨 prefrontal; Po. 眶后骨 postorbital; Qj. 方颧骨 quadratojugal; Sq. 鳞骨 squamosal; Tab. 棒骨 tabular

光滑，具不规则的网状雕饰。下颌缝合部长度适中，但较深。两下颌支夹角小，大约 30°。下颌在两犬齿处(距前端 2 厘米处)宽度 2.9 厘米，在下颌齿列末端(距前端 8 厘米处)宽度 5.7 厘米。这一组数字应能反映头骨眶前部相应部位的宽度，虽然后者要略宽于前者。夹板骨宽大，伸达缝合部之内。

下门齿全部断失，残留的齿基部可反映出牙齿的部分特征。每侧门齿 3 枚，第一齿最大，向后逐个减小。牙齿基部断面椭圆形。从向下倾斜的齿骨前缘可推测门齿是伸向前上方的。下颌具一对粗大的犬齿，断面椭圆形，从保存的齿基部可以推断犬齿是指向后上方的。犬齿的前后均没有明显的齿隙。左犬齿后齿列除最前面的 2 个齿冠未保存外，其余各齿都基本完整。第 1—第 8 犬齿后齿排成单行，呈现两个由小到大的旋回，后面还有 7 个牙齿(内 3 外 4)排成双行。同上颌齿一样亦是内侧牙齿大于外侧牙齿，其形态与上颌颊齿相

似。有趣的是下颌齿尖同样位于牙齿的前外侧，未见明显的磨擦痕迹。下颌齿式I3C1PC15。

下颌齿骨之后的部分在正模上保存得不甚完整，它与头骨咬合在一起，骨缝不清，无法详细描述。齿骨后端向后上方扬起，但似乎未伸达下颌的最高点喙状突(高约5.2厘米)。下颌后部表面未见骨片断失的痕迹，但也未见单独保存的隅骨的反射片(reflected lamina)。推测它紧贴在内侧的骨片上，一个几乎平行于下颌后端的骨缝也许就是证明。关节骨位于下颌下缘内侧，致使下颌关节低于下颌齿列一线。

比较与讨论 祁连双列齿兽以其高耸粗大的顶骨结节，独特的颊齿形态和双列齿系，有别与所有早期兽孔类动物，它代表一单独的新属新种是不成问题的。以往在有关大山口低等四足类动物群的文章中(Li and Cheng, 1995; 程政武等, 1995)都将这一标本归入恐头兽类，强调它与"*Syodon* 最为相似，后者的上颊齿单列，下颊齿双列"。在对化石作较为深入的观察和对比后，上述的提法似乎无法成立。叶菲莫夫幽齿兽(*Syodon efremovi* Orlov, 1958)在一些特征上，如中等大小的头骨，位于顶骨结节之上的大的顶孔，簇状分布的腭骨齿和翼骨齿，下颌的双齿列等方面与祁连双列齿兽相似。但幽齿兽在诸如眶间宽度大于间颞部宽度，顶孔两侧的凹(标示下颌收肌前端)可达额骨的后边缘，下颌门齿4枚，犬齿后齿低而侧扁等特征上与双列齿兽明显有别。双列齿兽的颊齿形态特异，更重要的是其眶后骨的前部出露在顶面，它的后侧部形成一明显的凹，在颞凹之内，下颌收肌前端延伸至此，它未达眶后骨的顶面，更无法延至额骨后缘。这一特征在分类上起着非常重要的作用。据 Hopson and Baughusen (1986)侧颞孔在后背方的扩大，以至背视可以见到外下颌收肌的起点区，是 Eotitanosuchia 和 Advanced therapsid 的共近裔性，它们以此特征有别于最原始的兽孔类 Biarmosuchia。而随着侧颞孔的加大外下颌收肌的起点进一步向前延伸出现在眶后骨的背面则是 Dinocephalia 的自近裔性。据此 *Biserodens* 与 eotitanosucians 在同一发展水平上，它无法被归入恐头兽类。与这一特征密切相关的是恐头兽类和其它进步的兽孔类间颞部进一步缩小，其宽度小于眶间宽度。而双列齿兽和始巨鳄类一样保持原始状态，间颞宽度大于眶间宽度。

除上述两个特征外，双列齿兽还在下列特征上与始巨鳄相似，它们的侧颞孔大于眼孔，眶后骨下支中止在眶弓中部，未伸达颧弓，间顶骨高而窄，后耳骨与方骨相接，腭骨和翼骨上具齿(这些特征不是它们所独有的，有些也出现在进步的兽孔类中)。但 *Biseridens* 与 *Eotitanosuchus* 二者间的差别是明显的。*Eotitanosuchus* 的头骨粗大，其长度约为 *Biseridens* 头骨的两倍；前者的眶前部长，约占头骨长度 66%(据 Chdinov, 1960 图1估算)，后者的眶前部长度适中，只占头骨全长的 44%；*Eotitanosuchus* 的顶孔小，*Biseridens* 的顶孔和顶骨结节之粗大，在兽孔类中几乎是无与伦比的；*Eotitanosuchus* 的上颌齿列中止在眼眶之前的一段距离，而 *Biseridens* 的上颌齿列延伸至眼眶之下；*Eotitanosuchus* 的上颌齿式为 I4–5 C1 PC8–9，颊齿小而平，呈单列，这与 *Biseridens* 非常独特的颊齿形态和双列齿列有很大区别。始巨鳄科的第二个属种 *Ivantosaurus ensifer* 的化石材料非常不完整，仅以一带有犬齿状齿的破碎上颌骨和方骨所代表，它与 *Biseridens* 的对比很难进行，但其粗大的犬齿状齿足以证明 *Ivantosaurus* 的个体比 *Biseridens* 要大得多。上述比较表明始巨鳄代表着一类体形巨大，肉食性的动物，而双列齿兽则是中等大小的食植物或杂食性的，这

些妨碍将 *Biseridens* 归入 Eotitanosuchidae，它可代表始巨鳄亚目中一个独立的新科 Biseridensidae。

Чудинов (1960)在首次确立始巨鳄超科(Titanosuchia)时，将它放在恐头兽亚目(Dinocephalia)中，Рождественский和Татаринов (1964)虽然没有接受超科这一分类单元，但也将始巨鳄科归入恐头兽亚目。Olson (1962)在研究北美和前苏联晚二叠世的陆生脊椎动物时将 *Eotitanosuchus* 与渐衰鳄 *Phthinosuchus* 一道归入一新建的始兽齿亚目(Eotheriodonta)，隶属兽齿亚目(Theriodonta)，认为它们是介于盘龙类(pelycosaurian)和兽孔类之间的肉食性的代表。Чудинов (1983)，Sigogneau-Russell (1989)与之持相同的观点。Romer (1967)，Carroll (1988)则将始巨鳄兽类包括 *Phthinosuchus*，*Biarmosuchus*，和 *Eotitanosuchus* 等放在兽孔目之下的一单独的 Eotitanosuchia 亚目中。Hopson and Baughusen (1986)对整个兽孔类进行了支序分类学的分析，结果表明 Eotitanosuchia 和 Biarmosuchia 代表最原始的兽孔类。*Biseridens* 在头骨的轻巧程度，无额骨，隅骨结节等方面较恐头兽亚目的貘头兽(*Tapinocephalus*)要原始，它似乎代表着最原始的食植物的兽孔类。就象恐头兽类包括肉食性的 titanosuchians 和食植物的 tapinocephalians 一样，由于 *Biseridens* 的加入 Eotitanosuchia 也包括两部分，食肉的 Eotitanosuchidae 和食植物或杂食的 Bideridensidae。

玉门大山口化石点含丰富的骨化石，从保存的头骨(包括近于完整的头骨和部分头骨骨片所代表的头骨)判断，在数量和种类上最为丰富的要属兽孔类，其次为迷齿两栖类和大鼻龙型类。迷齿两栖类的研究工作正在进行，尚未有正式报道，暂不作讨论。大鼻龙型类的材料虽然不少，但均为完整或不完整的牙床。作者(1995)依据牙齿形态，将其归入波罗蜥科(Bolosauridae)的一个发现于俄罗斯卡赞阶上部(II 带)的属种 *Belebey vegrandis*。这是大山口动物群中目前所发现的唯一外来种属。事实上大山口材料与俄罗斯的正模间在牙齿数量和大小，以及个别牙齿形态上存在差异。由于采自该化石点的相当部分材料尚未进行修理，目前的鉴定显然具有暂时性。我们期待着更完整的材料来证实或否定这一结论。

大山口动物群的兽孔类中含 2 属恐头兽类。其中 *Sinophoneus*(程政武等，1996)与俄罗斯 II 带的 *Titanophoneus* 最为相似；而 *Stenocybus*(程政武等，1997)，由于其小的个体，轻巧的头骨，小于眼孔的颞孔，未前移的下颌关节，和适当前伸的下颌收肌起点，被认为是最原始的恐头兽类，代表一单独的科 Stenocybusidae。本文记述的是大山口动物群中第 3 个兽孔类的科和属，它与俄罗斯 II 带的 *Eotitanosuchus* 最为相似。这样大山口动物群的已记述的 4 个成员或是在种属一级，或是在科、超科一级显示出与俄罗斯 II 带的密切关系。

近年来南非在原来的貘头兽带(*Tapinocephalus* Zone)之下又发现了一更原始的始二齿兽带(*Eodicynodon* Zone) (Rubidge, 1995a)。其中的恐头兽类 *Australosyodon* 和 *Tapinocaninus*，及二齿兽类的 *Patranomodon* 要分别比俄罗斯 II 带的 *Syodon*，*Ulemosaurus*，和 *Otsheria* 更原始(Rubidge, 1995b)。虽然 Rubidge (1995b)强调在晚二叠世时南北大陆的陆生脊椎动物可自由交换，但到目前为止南非的始二齿兽带尚未发现大鼻龙型类和始巨鳄类的成员，而始二齿兽带中的二齿兽类(dicynodonts)、丽齿兽类(gorgonopsian)和兽头类(therocephalian)也未出现在大山口动物群中，二者之间只共有恐

头兽类。由于大山口动物群的 *Sinophoneus* 比南非的 *Australosyodon* 稍进步，而 *Stenocybus* 比南非的 *Australosyodon* 原始，很可能这两个脊椎动物群处在相同的进化发展水平。

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FIRST DISCOVERY OF EOTITANOSUCHIAN (THERAPSIDA, SYNAPSIDA) OF CHINA

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Key words Yumen, Gansu, Late Permian, Eotitanosuchia Biseridensidae

Summary

Eotitanosuchia is a primitive suborder of Therapsida. Carroll (1989) included three families, Biarmosuchidae, Eotitanosuchidae and Phthinosuchidae in this suborder, while Sigogneau–Russell (1989) assigned only one family Eotitanosuchidae including two genera and two species. *Eotitanosuchus olsoni* Chudinov, 1960 and *Ivantosaurus ensifer* Chudinov, 1983. The two genera come from the Upper Kazanian, Esheevo Locality, Ocher Province, Russia. A recently discovered incomplete skull and mandibles from Upper Permian Xidagou Formation, Dashankou Locality, Gansu are described here as the first eotitanosuchian outside Russia. Associated with this taxon are numerous therapsids, labyrinthodont amphibians and captorhinomorphs, of which a bolosaurid *Belebey vegrandis*, two dinocephalians *Sinophoneous yumenensis* and *Stenocybus acidentatus* have been reported (Li and Cheng, 1995; Cheng and Ji, 1996; Cheng and Li, 1997). The discovery of eotitanosuchian in China further proves close relationships between the Dashankou Fauna and the Zone II of Russia, and provides new material for discussing the phylogeny of early therapsids.

Eotitanosuchia Boonstra, 1963

Biseridensidae Fam. nov.

***Biseridens* Gen. nov.**

Etymology *Biseri*–Latin "double rows"; *–dens* Latin word derived from Greek "odons", "teeth".

Diagnosis Primitive herbivorous or omnivorous therapsids with medium sized skull, narrow and short preorbital region, interorbital area depressed with a ridge along mid–line suture of frontals; intertemporal region wider than interorbital one, temporal fenestra larger than orbit; oval pineal foramen especially large, situated on high

parietal boss; lateral process of postorbital does not reach to zygomatic arch; a depression indicating origin area of muscle adductor mandibulae externus, present on the posterior portion of postorbital inside the temporal fossa; interparietal narrow and high; opisthotic contacts quadrate; palatal and pterygoid tuberosities bearing cluster of teeth, but transverse flange of pterygoid lacking teeth; lower jaw articulation posteriorly located and lower than dentition; cheek teeth unique shaped and double rowed on upper and lower jaw; lower formula I3 C1 PC15.

Biseridens qilianicus **Gen. et sp. nov.**

Etymology *qilian*–name of the mountain, on which the fossil was discovered.

Holotype An incomplete skull with posterior portion of left ramus of lower jaw (IGCAGS V 632).

Paratype Anterior part of lower jaws with complete dentition (IVPP V 12009).

Diagnosis Same as the genus

Description The type specimen is damaged in the regions of the snout, right lateral surface and palatal plate, but comparatively well preserved in the posterior portions of the dorsal and left surfaces, occipital plate and posterior part of left remus of the lower jaw. The paratype is comparable to the type specimen in size of teeth and width of dentary bone. The lower jaw was reconstructed (Fig. 1B) by overlying the posterior end of the left dentition of the paratype on its counterpart of the holotype. Similarly the anterior part of the snout was also reconstructed. As a result, estimative length of the skull is 18cm, and length of the lower jaw 16cm.

Judging from the preserved posterior portion, the shape of skull in dorsal view (Fig. 1A) is relatively narrow triangular. The preserved posterior part of the left nasal tapers posteriorly forming a wedge between the frontals at the level of the anterior margin of the orbits. The left lacrimal has been shifted inwardly by lateral pressure, and can not be seen in dorsal view. The left prefrontal with more or less opened suture with the nasal and frontal, is a protrusive bone on the antero–medial corner of the orbit in contrast with the slightly lifted borders of the orbits, the interorbital region is depressed, and the depression is subsequently divided into two parts by a ridge along mid–line suture of the frontals. The lateral process of the postorbital bone ends half–way down the postorbital bar. A depression indicating the area of origin of muscle adductor mandibulae externus is present on the posterior portion of the postorbital inside the temporal fossa. The pineal foramen is extremely large, oval, and situated on a stout parietal boss. The parietal is relatively short and broad. The intertemporal region is slightly wider than the interorbital one.

The shape of skull in lateral view can be reconstructed, although the anterior portion of the snout has lost and the preorbital region, postorbital bar and squamosal

have been slightly deformed (Fig. 1B). The preorbital region of the skull (8cm) is short, forming only 44 percent of the skull length. The temporal fenestra, enlarged by extending vertically and its medio-upper corner anteriorly, is larger than the orbit as in dinocephalians.

The preserved part of the maxilla is roughly triangular, and the dorsal portion which connects with the prefrontal is presumably the highest point of the whole maxilla. The maxilla with undulated lower margin extends back and meets the jugal beneath the orbit. A portion of tooth root with oval cross section 0.90 × 0.35cm appears in the broken anterior end of the maxilla. This is relatively large and presumably represents the left canine. There are 6 very special cheek teeth well preserved on the left maxilla. They are arranged in two rows, the inner row with 3 larger teeth is a little anterior to the outer row with 3 smaller teeth. The crowns of the teeth are low, stout oval in cross section and constricted at the basal portion. They have a short, blunt tooth point on the antero-labial side and an almost horizontal tooth facet surrounding the tooth point (Fig. 1C).

The left lacrimal is separated from the external naris by the maxilla and prefrontal as in most of early therapsids. The distinctly triradiate jugal extends upwards behind the orbit and contacts the posterior surface of the lateral process of postorbital. The posterior branch of the jugal meets the squamosal on lateral temporal bra, and extends backwards for a distance along the medial and ventral surface of the jugal process of squamosal. The ventral margin of the zygomatic arch lies at the same level as the lower margin of the maxilla and does not emarginate posteriorly as anomodonts. The main body of the squamosal stretches posto-laterally and a narrow tape-like oblique surface of the squamosal below the medial margin of the temporal fossa is present, and does not appear in the other therapsids. Its functional significance is unknown. The left quadratojugal is completely preserved, but its sutures with the squamosal and quadrate could not be determined. The lower jaw articulation is not anteriorly positioned and lies on a lower level than that of upper jaw dentition.

The occipital plate is reasonably preserved, but individual bones can be distinguished only by surface texture as sutures are not visible (Fig. 2A). The interparietal, a large bone which is higher than its width, has a mid-line ridge which expands dorsally and ventrally, and on the ventral side ends at the suture with the supraoccipital. The wide and low supraoccipital encloses the foramen magnum from dorsally. The foramen magnum has lost its original shape, but judging from the left side, it seems to be a large and relatively wide arched fenestra. The tripartite occipital condyle consists of the left and right exoccipital and basioccipital. The tabular bone with irregular contour occupies quite a large area lateral to the interparietal and supraoccipital. The stout paroccipital process contacts the quadrate laterally. The parietal,

postorbital, squamosal and quadratojugal are visible on the occipital plate to varying degrees.

The ventral surface of skull has been badly dameged, but some features can be recognized from several isolated incompletely preserved bones. The right stapes together with the articulation part of quadrate, is a comparatively stout bone with both ends being expanded and having a constricted middle portion. Both palatines are incompletely preserved. The left palatine bears 9 slightly large teeth while the right one has 10 larger and 5 smaller teeth (Fig. 2C). A small piece of bone scattering with small teeth seems to represent the left pterygoid (Fig. 2B). No teeth are present on the transverse flange of pterygoid.

The paratype, the anterior part of the lower jaws, has a deep symphysial region and a small angle of about 30° between the two lower jaw rami (Fig. 2D, 2E). The upper margin of mandible is undulated in lateral view and the anterior portion in front of the canine inclines forwards gently. The dentary is relatively deep and short. The large splenial extends forward and enters the symphysial region. None of the crowns of the incisor and canine teeth are preserved, but the bases of the teeth indicate clearly 3 incisors with an oval cross–section on each side. The first incisor is the largest, and they become smaller backwards. The oblique anterior margin of the dentary implies that the incisors may extend forwards and upwards. The canine appears to be quite large and points upwards and backwards. There is no diastema both in front and at the back of the canine. The 8 anterior postcanines line a single row while the other 7 teeth are arranged in double rows (3 inner and 4 outer). Since the lower teeth in double rows are similar to the upper cheek teeth not only in shape, but also in the position of the tooth point, and no wearing facet has been found, their cutfunction is still a mystery. The formula of the lower dentition is I3 C1 PC15.

It is difficult to describe the posterior part of lower jaw in detail because of the tight occlusion with the skull and invisible sutures in the holotype. The posterior end of the dentary extends backwards and upward, but does not reach the coronoid process (5.2cm high) of lower jaw. The articulation is ventrally positioned, so that the lower jaw articulation is below the level of the dentition.

Comparison and discussion In having an extremely high and stout parietal boss, very special shaped cheek teeth arranged in double rows, *Biseridens qilianicus* is distinguished from all the other early therapsids, and represents a new genus and species. In the previous reports (Li and Cheng, 1995; Cheng *et al.*, 1996), the specimens of *Biseridens qilianicus* were considered as a dinocephalian closely related to *Syodon efremovi* from Upper Permian Isheevo of Russia. In some features, medial sized skull, very large pineal foramen, temporal fenestra being larger than orbit, double rows of teeth in lower jaw, *Syodon* somewhat resembles *Biseridens*, from

which it differs in having 4–5 incisors, low and lateral compressed postcanine, intertemporal region being narrower than interorbital one, the depression indicating the origin of muscles mandible adductor externus (MAME) reaching the posterior border of the frontal on the dorsal surface of temporal roof. In fact, *Biseridens* with the origin of MAME on the posterior part of the postorbital inside the temporal fossa, rather than on dorsal surface of temporal roof, including surface of postorbital bar as in dinocephalian, is on an equal level with eotitanosuchian. The intertemporal region becomes more narrow than interorbital region in dinocephalian and other advanced therapsids, but it remains wider than interorbital region in *Biseridens* and eotitanosuchians.

Besides the two characters mentioned above, *Biseridens* also resembles the eotitanosuchian in the lateral temporal fenestra being larger than the orbit; having high and narrow postorbital; the opisthotic contacting the quadrate; presence of clusters of teeth on the palatine and pterygoid (the features are not unique to them, sometimes also exist in other advanced therapsids). However, *Biseridens* differs from *Eotitanosuchus* in following respects, the skull of *Eotitanosuchus* is larger and stouter, almost two times of that of *Biseridens* in size; the preorbital region is longer, 66 percent of the skull length in *Eotitanosuchus*, but only 44 percent in *Biseridens*; in contrast to smaller pineal foramen of *Eotitanosuchus*, its counterpart in *Biseridens* is extremely lerge; the dentition ends anterior to the orbit in *Eotitanosuchus*, but extends more backwards to a point beneath the orbit in *Biseridens*; unlike *Biseridens*, the upper cheek teeth in *Eotitanosuchus* are small, single rowed, the tooth formula I4–5 C1 PC8–9. It is very difficult to compare *Biseridens* with *Ivantosaurus*, as the latter is based on very fragmentary material. The type specimen of *Ivantosaurus*, a broken maxilla with very strong canine implies that the size of *Ivantosaurus* as *Eotitanosuchus* is much larger than that of *Biseridens*. Based on the analysis above, *Biseridens*, as a herbivore or omnivore, is sufficiently different from the large sized carnivorous members of the Eotitanosuchidae, to warrant its allocation to a new family.

In the Dashankou lower tetrapod fauna, therapsids are more abundant in quantity and variety, then labyrinthodont amphibians and captorhinomorph bolosaurids. The bolosaurid material, represented by many incomplete jaw bones with teeth, were assigned to *Belebey vegrandis*, a species from Zone II of Russia, although they are different from the type specimen in number and size of teeth and shape of the 3rd tooth (Li and Cheng, 1995). The identification seems to be tentative for the incompleteness of the specimens and further conclusions can only be made once more complete fossils are discovered. Among the therapsids of Dashankou fauna, the dinocephalian *Sinophoneus* (Cheng and Ji, 1996) resembles *Titanophoneus*, a genus from Zone II of Russia and *Stenocybut* (Cheng and Li, 1997) was considered as the

most primitive dinocephalian and represented an independent family Stenocybusidae. The third therapsid genus. *Biseridens* is related to Russian *Eotitanosuchus*, though based on which a new family Biseridensidae is proposed in the present paper.

There was rather free faunal interchange between Laurasia and Gondwana during the Late Permian (Rubidge, 1995b), but bolosaur captorhinomorph and eotitanosuchian have not been reported from *Eodicynodon* Zone and *Tapinocephalus* Zone of South Africa and dicynodonts, gorgonopsian and therocephalian, the elements of *Eodicynodon* Zone and *Tapinocephalus* Zone, have not been found in Dashankou fauna. Dinocephalians are the only group shared by the two regions, China and South Africa, among which *Sinophoneus* is more primitive than *Anteosaurus* from *Tapinocephalus* Zone and more advance than *Australosyodon* from *Eodicynodon* Zone, and *Stenocybus* is more primitive than *Australosyodon*. With the exception of labyrinthodont amphibians which are still being studied, the therapsids and bolosaur of the Dashankou lower tetrapod fauna suggest that the fauna is more closely related to the Zone II of Russia than to *Tapinocephalus* Zone and *Eodicynodon* Zone of South Africa.

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图版说明 (Explanations of plates)

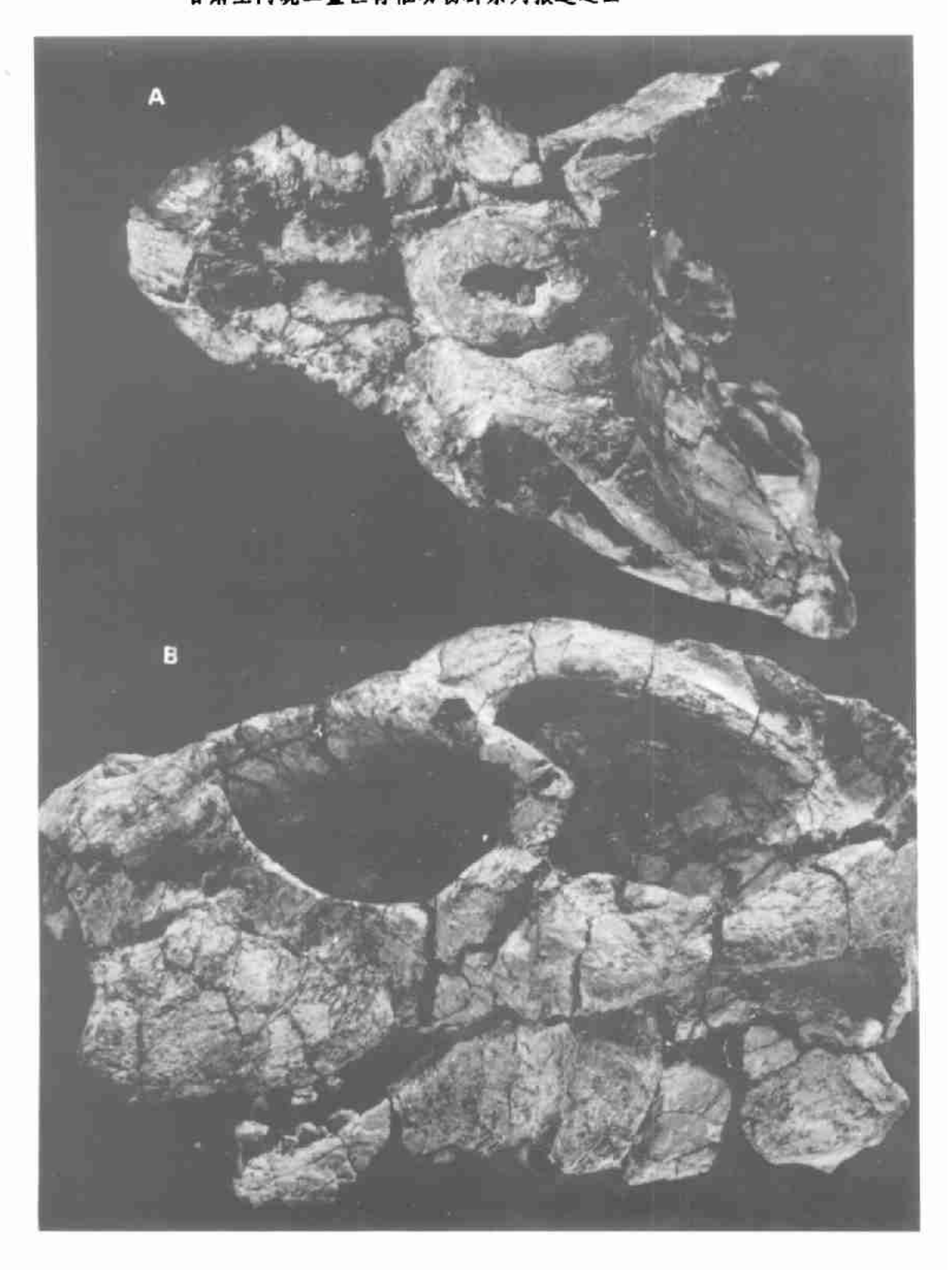
图版 I (plate I)

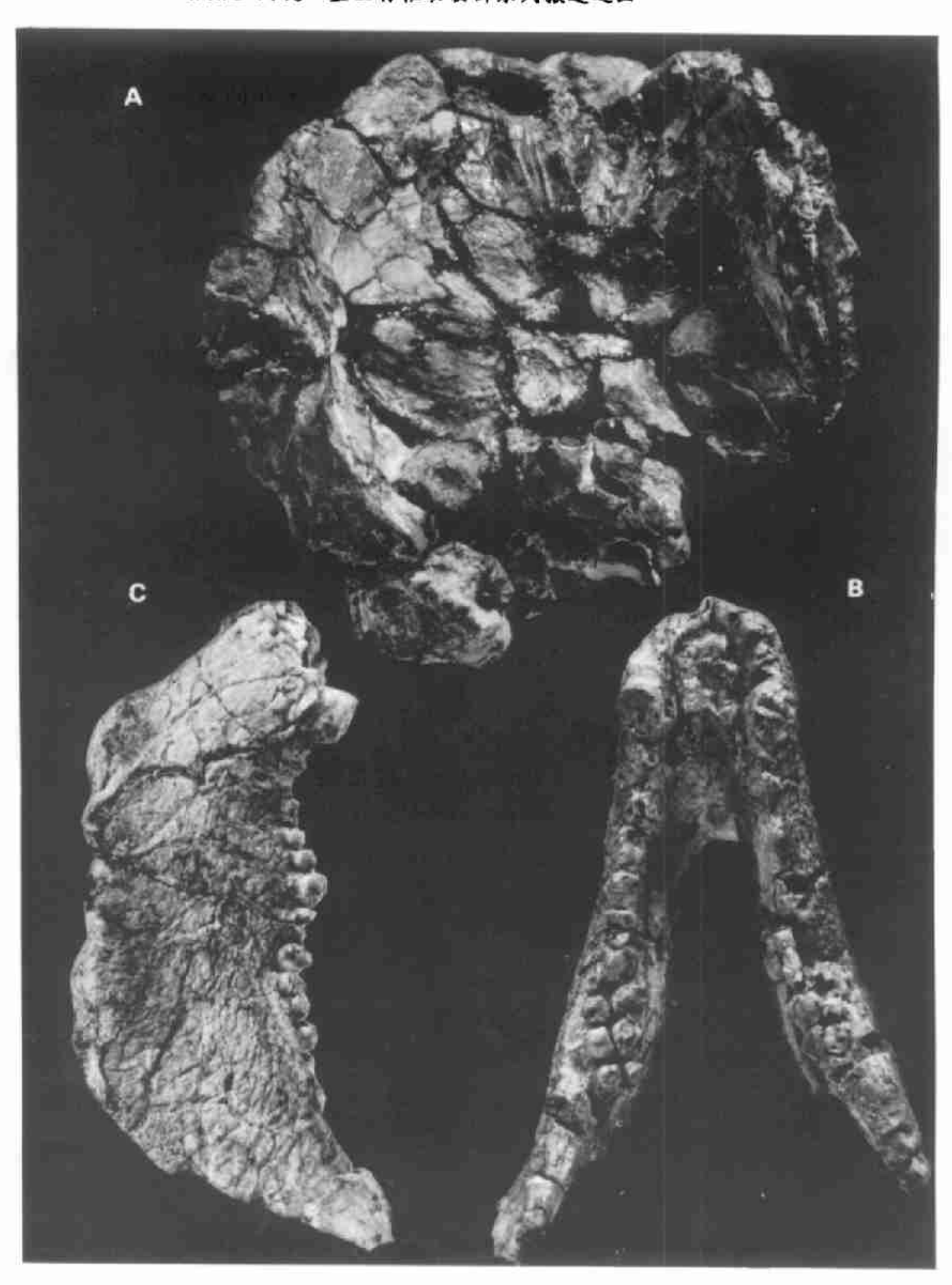
祁连双列齿兽 *Biseridens qilianicus* gen. et sp. nov. (Holotype IGCAGS V362) 原大 (natural size)

A. 头骨背视 skull in dorsal view; B. 头骨及下颌侧视 skull and lower jaw in lateral view

图版 II (plate II)

祁连双列齿兽 *Biseridens qilianicus* gen. et sp. nov. (Holotype IGCAGS V 362. Paratype IVPP V 12009) 原大 (natural size). A. 头骨枕视 skull in occipital view; B. 下颌背视 lower jaw in dorsal view; C. 下颌侧视 lower jaw in lateral view


A
B


A
C
B